SYNONYMY OF THREE PESTIFEROUS *MATSUCOCCUS* SCALE INSECTS (HEMIPTERA: COCCOIDEA: MATSUCOCCIDAE) BASED ON MORPHOLOGICAL AND MOLECULAR EVIDENCE

JANIE M. BOOTH AND PENNY J. GULLAN

Department of Entomology, University of California, 1 Shields Avenue, Davis, CA 95616-8584, U.S.A. (e-mail: pjgullan@ucdavis.edu)

Abstract.—The scale insect genus Matsucoccus Cockerell (Coccoidea: Matsucoccidae) contains several economically important species that cause damage to pine trees, Pinus species, in the United States and elsewhere in the Holarctic Region. Efforts to reconstruct the phylogeny of the group have provided information on genetic variation within and among species. Here, three species of Matsucoccus are synonymized based on newly acquired molecular data and reassessment of morphological data. Matsucoccus resinosae Bean and Godwin, described from the eastern United States, and Matsucoccus thunbergianae Miller and Park, from South Korea, are considered to be **new synonyms** of Xylococcus (now Matsucoccus) matsumurae Kuwana. The taxonomic confusion surrounding these names is discussed. In addition, we suggest that several other species of Matsucoccus, including M. pini Green, should be investigated as possible synonyms of M. matsumurae.

Key Words: Margarodidae, Matsucoccus, red pine scale, taxonomy

Matsucoccus Cockerell is a morphologically conservative group of scale insects placed either in the scale insect family Margarodidae (Ben-Dov et al. 2005) or in its own family, Matsucoccidae (Koteja 1984, 1986; Foldi 2004). All species feed exclusively on *Pinus* (Pinaceae) and are mainly Holarctic, with limited records from the Neotropical and Indotropical regions (Ben-Dov 2005, Ben-Dov et al. 2005). This genus has received moderate taxonomic treatment (Ray and Williams 1984, 1991; Gill 1993; Foldi 2004), and 34 extant species are recognized (Ben-Dov 2005).

Recent research to reconstruct the phylogeny of *Matsucoccus* has provided the first hypothesis of species relationships based on molecular and morphological data (Booth, Cook and Gullan,

unpubl. data). One relationship of particular interest is that of three pest species, Matsucoccus matsumurae (Kuwana), the Japanese pine bast scale, M. resinosae Bean and Godwin, the red pine scale, and M. thunbergianae Miller and Park, the black pine bast scale. New evidence supports the synonymy of the three species. Entomologists have speculated that M. matsumurae and M. resinosae are synonymous (Ray 1982; McClure 1983b, 1987; Foldi 2004). The recent catalogue of Margarodidae (Ben-Doy 2005) treats these two species separately, but mentions previous work suggesting that M. resinosae may be a junior synonym of M. matsumurae (McClure 1983a, Young et al. 1984, Park et al. 1986).

Matsucoccus resinosae infests red pine, Pinus resinosa, on the east coast of the United States. Red pine scale was first recognized in 1946 in Easton, Connecticut (Plumb 1950), and its rapid spread and the high tree mortality that it caused suggested that it was a new introduction (Bean and Godwin 1955). It has been hypothesized that it was introduced during the 1939 New York World Fair on exotic pines imported as a display, because the same truck that transported the exotic pines from the port was used to transport red pines from Easton to the fairgrounds (Doane 1959). The feeding cyst stage of M. resinosae can damage the needles, causing extensive flagging and needle drop (McClure 1976, Duda 1977). Damage is particularly severe in plantations found south of red pine's native range (Bean and Godwin 1955), apparently because low winter temperatures in the pine's natural range to the north prevent survival of red pine scale nymphs (Doane 1959; McClure 1983a, b). Damage from the red pine scale has resulted in almost complete removal of once abundant red pine plantations in Connecticut and New York states and it is now difficult to locate intact stands (J. Booth pers. observation, Providence Water Supply Board 2005).

The Japanese pine bast scale, *M. matsumurae*, has similar biology and morphology to *M. resinosae* (McClure 1976, 1983a). This scale is a pest in Asia, especially on black pine, *Pinus thunbergii* (Taketani 1972, Cheng and Ming 1979). The species was described originally by Kuwana as *Xylococcus matsumurae* (Kuwana 1905, 1907), and later transferred to *Matsucoccus* by Cockerell as the type species of his new genus (Cockerell 1909).

The third species, *M. thunbergianae* Miller and Park, from South Korea, was described as similar to *M. matsumurae* and *M. resinosae* (Miller and Park 1987). It is not possible to distinguish *M.*

thunbergianae from M. matsumurae and M. resinosae, based on the adult females or the first-instar nymphs, but Mthunbergianae is said to differ from the other two species in the size of the adult male, in the number of generations per year, and in overwintering as the secondinstar nymph (as the first-instar nymph in the other two species). Matsucoccus thunbergianae is univoltine or has only a partial second generation (Miller and Park 1987), whereas M. matsumurae and M. resinosae are bivoltine or have a partial third generation (McClure 1977, Miller and Park 1987). Matsucoccus thunbergianae is considered a pest in Korea on black pine (Miller and Park 1987, Chung et al. 2000).

Several available pieces of biological evidence support the synonymy of these three Matsucoccus species. First, the sex pheromones of M. matsumurae. Mthunbergianae, and M. resinosae have been shown to be cross attractive in bioassay studies (Young et al. 1984, Park et al. 1986). The primary component of the sex attractant was identified and the pheromone is identical for the three species and has been named "matsuone" (Lanier et al. 1989, Hibbard et al. 1991). Second, all species occur on hosts found in the same Pinus subsection, subsection Pinus, of the pine tree phylogeny of Gernandt et al. (2005). Matsucoccus matsumurae occurs on seven Pinus species (McClure 1983a), Matsucoccus thunbergianae only on P. thunbergii and P. densiflora (Miller and Park 1987), and M. resinosae is found on P. resinosa (Kuwana 1905, Bean and Godwin 1971, Miller and Park 1987), which is the only species of the Pinus subsection Pinus in the United States (Gernandt et al. 2005). Ray (1982) and McClure (McClure 1983b) went further and noted that M. resinosae and M. matsumurae are more specifically found only on members of the Sylvestres group of the subsection Pinus. However, the Sylvestres group is

Species Name	# Slides (# Females)	Collection Information	Depository
M. matsumurae	l (l non-type)	JAPAN: Kanagawa-ken, ex pine tree, 13.v.1919; Coll. S. I. Kuwana (mounted from dry material sent by Kuwana to F. B. Herbert)	BME
	1 (2 non-type)	JAPAN: Nagashima, ex <i>P. densiflora</i> , 10.v.1970; Coll. M. Inoure	BME
	2 (2 non-type)	JAPAN: Nagashima, ex <i>P. densiflora</i> , 4.v.1970; Coll. M. Inoure	USNM
	3 (4 non-type)	JAPAN: Japan: Mie Prefecture, Shimagahara Village, ex <i>P. thunbergii</i> ; 24.ii.2004; Coll. T. Kondo	BME
M. pini	3 (5 paralectotypes)	ENGLAND: Oxshott, Surrey, ex <i>P. sylvestris</i> , 31.x.1922; Coll. F.C. Withycombe	BMNH
M. resinosae	3 (holotype and 2 paratypes)	USA: Connecticut, Easton, ex <i>P. resinosa</i> , 2.v.1948; Coll. George H. Plumb	USNM
M. thunbergianae	4 (holotype and 5 paratypes)	SOUTH KOREA: Kohung, Chollanam-do, ex <i>P. thunbergiana</i> (now <i>P. thunbergii</i>), collected xii.1983, lab reared iv.1984; Coll. S. C. Park	USNM
	l (2 paratypes)	SOUTH KOREA: Kohung, ex <i>P. thunbergii</i> , collected xii.1983, lab reared iv.1984; Coll. S. C. Park	BME

Table 1. Specimens of adult females examined for morphological analysis.

not recognized in the most current *Pinus* phylogeny (Gernandt et al. 2005). Third, the distribution of *M. matsumurae*, *M. resinosae* and *M. thunbergianae* supports their synonymy. McClure (1983b) pointed out that the first two species are restricted to a similar northern latitudinal limit: 41°50'N in the U.S., 41°30'N in Japan, and 41°30'N in China. Similarly, *M. thunbergianae* has been reported only from South Korea (Miller and Park 1987), for which the northern boundary lies at about 39°N.

Here we present the first molecular data and reassess the morphological evidence to show that specimens described as *M. matsumurae*, *M. resinosae* and *M. thunbergianae* belong to the same species. We synonymize *M. resinosae* and *M. thunbergianae* under the senior synonym *M. matsumurae* and provide a new diagnosis for this species.

MATERIALS AND METHODS

Morphology.—Morphological characters were evaluated and measured using a Leica compound microscope. Type material was examined for M. resinosae and M. thunbergianae, whereas subsequent material collected by the original author was studied for M. matsumurae (see below under "Type material"; also Table 1). Specimens from each collection were scored for 14 morphological characters (Table 3), including those previously recognized by Ray (1982). The diagnosis was prepared based on the specimens listed in Table 1. Specimens examined are housed at the Bohart Museum of Entomology (BME), University of California, Davis; The Natural History Museum, London (BMNH); and the Coccoidea Collection of the National Museum of Natural History, Smithsonian Institution (USNM) in Beltsville, Maryland.

Genetic analysis.—Molecular data were acquired for 13 specimens belonging to six named *Matsucoccus* species that the authors field collected or that colleagues donated (Table 2). Specimens were stored in 75% ethanol for slide mounting and 100% ethanol for molecular work. Genomic DNA was extracted

tsoH suniq		Life Stage	Coordinates	Collection Information	DNA Code	ounk soloods	8
sijnpə	`d	adult female	M.SE 211 N.62 #E	AZ Yavapai Co: Copper Basin Rd, 6 miles E of	1WB037	snidsipop	W
	-			Skull Valley; 30.iii.2005; Coll. J. Booth			
sijnpə	ď	adult female	M110711 'N77404E	AZ Yavapai Co: 1.5 mi W of Mingus Mtn Pass,	1WB038	snidkipoov	\mathcal{W}
manuonom	đ	squuru	M195.811 N10V VE	0100 May 89; 2010, 2002; Coll. J. Booline	oroanti		1
mindonom	a . 1	suduku	A OC OLL 'N 45 50	CA Netil Co. Flazici Faix, 7.2001, Con. J. Nency	0+09 MI	snidsipop	71
nsoismiod	· 1	suduku	M OC 171 'NI 97 05	Ridge Rd - 2 iv 2004. Colle 1 Booth and T Kondo	CLORING	sns01əsiq	.71
<i>ns0</i>	d	6008	MICU.ICI NICI 68	Vidge rui, z.w.2004, Cons. J. Boon and T. Wondo	900aMI	suscrasiq	11
hermon		6330	A TO 171 'N TI (C	Park: 9 iv 2004: Coll I Booth	OZOGIALC	enconsein	. 71'
inotinot	d	syduxu	M.SZ 911 N.ZS ZE	CA San Diego Co: Mt. Laguna. Cleveland National	6008ML	susotasid	11
		and the Co		Forest Visitor's Center: I.v.2004: Coll. J. Booth	(200102	0120012010	
nbigin	ď	adult female	40°52'N, 72°48'W	NY Suffolk Co: Manorville, Hwy 495, exit 70;	1MB023	snjozijipg	W
				10.ix.2004; Coll. D. Gilrein			
vpigir	d	cyst	M168°27, N128°04	NY Suffolk Co: Riverhead, East Moriches	1WB054	snlo2illn8	\mathcal{W}
				Riverhead Road; i.ix.2004; Coll. J. Booth			
กแก้เก่ยา่ง	d	รธิธิจ	M.ES 92 N.10 68	MD Prince Georges' Co: Beltsville, USNM facility;	1WB036	snjosijjnž	11
	u		dicoster itist re	8.iii.2005; Colls. J. Booth and D. Miller			
n8.oqump	·d	alamat fluba	34 40.N' 130.03.F	Japan: Mie Prefecture, Shimagahara Village;	1/1801	əp.muns1mu	TV
iione que que que	a	<i>40110</i>	Sher ser Noe er	C411.2004; Coll. 1. Kondo	LIUGINI		,,
แ&เวอนทนา	·	1860	∃ / L C7 L 'NL 07 7₩	China: Yiong County in Jim Province, ivormeast	/ tog tail	อบภานเกรายนเ	.71'
Dsouisər	d	1872	M, 77. EL N, 15. 17	ULA NY Durchess Co. I afavetteville I afavetteville	2008MI	<i>dbsouisda</i>	IN
20010001		2010	N'IL CLEATICAT	Multiple Use Area: 8.ix.2004; Coll. J. Booth	CTOTHE	200010021	
рѕощѕәл	ď	alamaî fluba	W'91 ET N'10 04	USA. CT Litchfield Co: Canaan, junction of Under	1WB030	<i>әрѕоція</i> әл	W
				Mountain and Cobble Roads; 27.viii.2004; Coll. C.			
				Maier			
iigrodnudt	d	adult female	32 01/N, 126 43/E	South Korea: Naju City, Chollanamdo; 4.iii.2005;	1708MU	อทนทุธิงอินุนทนุเ	W
				Coll. SC. Park			
	лгон кличч 120 клича 120	 120 Н гилия Нолея Р. еслийся Р. солисегоса Р. солисегоса Р. солисего Р. гізіда Р. тізіда Р.	Life Stage Prints Hoat Life Stage Prints Hoat adult female P. edulis nymphs P. edulis nymphs P. edulis rigida eggs P. rigida eggs P. rigida edult female P. rigida rigida eggs P. rigida eyst P. resinosa resinosa P. resinosa P. resinosa eyst P. resinosa P. resinosa resinosa P. resinosa P. resinosa P. resinosa P. resinosa P. resinosa P. resinosa P. resinosa P. resinosa P. resinosa	Соолбілалея Life Stage Рипик Ноя. Соолбілалея Life Stage Рипик Ноя. 34, 29'W, 112 35'W adult female P. edulis 40 01'W, 121 55'W nymphs P. edulis 40 01'W, 121 55'W nymphs P. vivginda 40 52'W, 121 55'W adult female P. edulis 40 52'W, 121 55'W adult female P. vivginda 40 55'W, 121 55'W adult female P. vivginda 40 55'W, 121 55'W adult female P. vivginda 40 55'W, 121 55'W adult female P. vivgina 40 55'W, 121 55'W adult female P. vivgina 40 55'W, 121 02'W cysi P. vivgina 40 55'W, 121 02'W cysi P. vivgina 40 55'W, 121 02'W cysi P. vivgina 40 55'W, 120 55'W adult female P. vivgina 40 55'W, 120 56'W P. vivgina P. vivgina 40 55'W Cysi P. vivgina 40 55'W Cysi P. vivgina 40 6'W P. vivgina 40 7'W <td< td=""><td>Collection Information Conditionates Life Stage Punk Host AZ Yavapri Co: Coppet Bain R4, 6 miles E of Skul Valley; 30,iii.2005; Coll. J. Booth 34, 29'N, 112, 35'W adult female P. edults AZ Yavapri Co: Coppet Bain R4, 6 miles E of Skul Valley; 30,iii.2005; Coll. J. Booth 34, 29'N, 112, 35'W adult female P. edults AZ Yavapri Co: Coppet Bain, R4, 6 miles E of Kidge R4; 2,iv.2004; Coll. J. Booth 34, 42'N, 112, 35'W adult female P. monophylla CA Kern Co: Fraiter Park; 7.2001; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. monophylla CA Kern Co: Fraiter Park; 7.2001; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. monophylla CA Kern Co: Fraiter Park; 7.2001; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. monophylla Ridge R4, 2, iv.2004; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. virginan NY Suffolk Co: Manoville, Hwy 495, exit 70; 40'S'N, 72'39'W eyst P. virginan Riverhead Road: i, ix.2004; Coll. J. Booth 32, 5'N, 116, 5'N, 73'39'W eyst P. virginan Riverhead Road: i, ix.2004; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. virginan Riverhead Road: i, ix.2004; Coll. J. Booth 32, 2'N, 125'7'N, 73'39'W eyst P. virginan Riverhead Road: i, in, 2004; Coll. J. Booth 32, 5'N, 12'5'7'N, 73'4</td><td>DNA Gode Conditates Life Stage Pinue Hoat DNA Gode Collection Information Conditates Life Stage Pinue Hoat JMB037 AZ Yarapai Co: Copper Basin Rel 6 miles E of 34, 29'N, 112 35'W adult fermale P. edults Skull Valley; 30(ii),2005; Coll. J. Booth Skull Valley; 30(ii),2005; Coll. J. Booth 34, 49'N, 112 35'W adult fermale P. edults JMB038 AZ Yarapai Co: Laria Vo f Mingue Min Pass, 34'42'N, 112'11'W adult fermale P. edults JMB036 CA Kerada Co: Sinigletown 324'42'N, 112'02'W mymphis P. orothoris JMB013 CA Nerada Co: Sinigletown 32'5'N, 112'02'W adult fermale P. edults JMB026 CA Nerada Co: Sinigletown 32'5'N, 112'02'W adult fermale P. orothors JMB013 Collis L, Stoth; Coll, J. Booth 32'5'N, 112'02'W adult fermale P. rigida JMB014 China, Stott; Coll, J. Booth 32'5'N, 112'02'W adult fermale P. rigida JMB025 CA State Releved Coll, J. Booth 32'5'N, 112'02'W ry Withor P. rigida JMB024</td><td> Disclosus JMB037 AZ Yavapai Co: Operendinational Coordinates Life Stage Point Heart deutyphils JMB037 AZ Yavapai Co: Operendinational Coordinates Life Stage Point Heart deutyphils Skull Valley; 30iii.2005; Coll. J. Booth Acad. Co: On M.L. guant. Plant Reviews devine State Co: M.L. guant. Coll. J. Booth Acad. Co: On M.L. guant. Coll. J. Booth Acad. Co: Coras. Valley: Animale Matternational Acad. Co: Coras. Valley: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: Coras. Valley: Acad. So: Acad. Co: Coras. Valley: Acad. So: Acad. Co: Coras. Valley: Acad. So: Acad. Co: Coras. M.L. Acad. So: Acad. So: Acad. Co: Coras. M.L. Acad. So: Acad. Co: Manorville, Hwy 495, exit. 700; 40: S2'N, 72'48'W. adult female P. Animbergi Micelins. JMB025 MB025 MB024 MB025 MB025 MB024 MB025 MB025 MB024 MB025 MB025</td></td<>	Collection Information Conditionates Life Stage Punk Host AZ Yavapri Co: Coppet Bain R4, 6 miles E of Skul Valley; 30,iii.2005; Coll. J. Booth 34, 29'N, 112, 35'W adult female P. edults AZ Yavapri Co: Coppet Bain R4, 6 miles E of Skul Valley; 30,iii.2005; Coll. J. Booth 34, 29'N, 112, 35'W adult female P. edults AZ Yavapri Co: Coppet Bain, R4, 6 miles E of Kidge R4; 2,iv.2004; Coll. J. Booth 34, 42'N, 112, 35'W adult female P. monophylla CA Kern Co: Fraiter Park; 7.2001; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. monophylla CA Kern Co: Fraiter Park; 7.2001; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. monophylla CA Kern Co: Fraiter Park; 7.2001; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. monophylla Ridge R4, 2, iv.2004; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. virginan NY Suffolk Co: Manoville, Hwy 495, exit 70; 40'S'N, 72'39'W eyst P. virginan Riverhead Road: i, ix.2004; Coll. J. Booth 32, 5'N, 116, 5'N, 73'39'W eyst P. virginan Riverhead Road: i, ix.2004; Coll. J. Booth 32, 2'N, 112, 35'W adult female P. virginan Riverhead Road: i, ix.2004; Coll. J. Booth 32, 2'N, 125'7'N, 73'39'W eyst P. virginan Riverhead Road: i, in, 2004; Coll. J. Booth 32, 5'N, 12'5'7'N, 73'4	DNA Gode Conditates Life Stage Pinue Hoat DNA Gode Collection Information Conditates Life Stage Pinue Hoat JMB037 AZ Yarapai Co: Copper Basin Rel 6 miles E of 34, 29'N, 112 35'W adult fermale P. edults Skull Valley; 30(ii),2005; Coll. J. Booth Skull Valley; 30(ii),2005; Coll. J. Booth 34, 49'N, 112 35'W adult fermale P. edults JMB038 AZ Yarapai Co: Laria Vo f Mingue Min Pass, 34'42'N, 112'11'W adult fermale P. edults JMB036 CA Kerada Co: Sinigletown 324'42'N, 112'02'W mymphis P. orothoris JMB013 CA Nerada Co: Sinigletown 32'5'N, 112'02'W adult fermale P. edults JMB026 CA Nerada Co: Sinigletown 32'5'N, 112'02'W adult fermale P. orothors JMB013 Collis L, Stoth; Coll, J. Booth 32'5'N, 112'02'W adult fermale P. rigida JMB014 China, Stott; Coll, J. Booth 32'5'N, 112'02'W adult fermale P. rigida JMB025 CA State Releved Coll, J. Booth 32'5'N, 112'02'W ry Withor P. rigida JMB024	 Disclosus JMB037 AZ Yavapai Co: Operendinational Coordinates Life Stage Point Heart deutyphils JMB037 AZ Yavapai Co: Operendinational Coordinates Life Stage Point Heart deutyphils Skull Valley; 30iii.2005; Coll. J. Booth Acad. Co: On M.L. guant. Plant Reviews devine State Co: M.L. guant. Coll. J. Booth Acad. Co: On M.L. guant. Coll. J. Booth Acad. Co: Coras. Valley: Animale Matternational Acad. Co: Coras. Valley: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: M.L. guant. Coll. J. Booth Acad. So: Acad. Co: Coras. Valley: Acad. So: Acad. Co: Coras. Valley: Acad. So: Acad. Co: Coras. Valley: Acad. So: Acad. Co: Coras. M.L. Acad. So: Acad. So: Acad. Co: Coras. M.L. Acad. So: Acad. Co: Manorville, Hwy 495, exit. 700; 40: S2'N, 72'48'W. adult female P. Animbergi Micelins. JMB025 MB025 MB024 MB025 MB025 MB024 MB025 MB025 MB024 MB025 MB025

Table 2. Specimens used for molecular analysis.

using a Qiagen DNeasy® kit (Qiagen Inc., Valencia, California, U.S.A.). DNA was extracted non-destructively in many samples so that the cuticle could be saved for identification. In the remaining cases, a dead adult female found in association with the other life stages used for DNA extraction was preserved and mounted for identification. Identification was performed using published keys and descriptions (Kuwana 1905, Bean and Godwin 1955, Ray 1982, Miller and Park 1987, Foldi 2004) supported by knowledge of each species' known distribution and host-plant(s) and, in the case of M. thunbergianae, by the authorative identification of Seung-Chan Park who was one of the describers of this species (Miller and Park 1987). Standard methods for scale insect DNA analysis were utilized for molecular work (Cook et al. 2002, Downie and Gullan 2004). Targeted DNA sequences (Table 4) were obtained using Polymerase Chain Reaction, gel agarose DNA visualization, and automated DNA sequencing at the UC Davis Division of Biological Sciences DNA Sequencing Facility. Sequences were edited in Sequencher version 4.0.5 (Gene Codes Corp, Ann Arbor, Michigan, U.S.A.) and aligned in Se-Al (Rambaut 1996). PAUP* (Swofford 2003) was used for determining pairwise differences among species of Matsucoccus. As part of a larger phylogenetic project, sequence data from two nuclear ribosomal genes were analyzed (Booth, Cook, and Gullan, unpublished data). The markers examined were the small subunit ribosomal gene (SSU rDNA or 18S) and the D2, D3 and D10 expansion regions of the large subunit ribosomal gene (LSU rDNA or 28S) for a total of approximately 2,070 base pairs. These sequences were aligned and compared to assess the amount of genetic difference between purported species. Polymorphic sites within individuals were identified by examining electropherograms in Sequencher 4.0.5. Electropher-

ograms of individuals within species were aligned in Sequencher 4.0.5 and examined to identify variable sites and indels.

RESULTS AND DISCUSSION

Molecular evidence supports the synonymy of *M. matsumurae* and *M. resinosae* with the new inclusion of *M. thunbergianae*. Morphological analysis corroborates this information - no discernible consistent morphological differences are observed.

Nucleotide sequence data.-Matsucoccus matsumurae, M. resinosae, and M. thunbergianae had identical sequences for the18S and 28S D10 regions. The D2-D3 region of 28S revealed a total of four polymorphisms among these three species. This amount of divergence is similar to that seen in other Matsucoccus species in terms of polymorphic sites or intraspecific divergence, as exemplified by M. acalyptus Herbert, M. bisetosus Morrison, and M. gallicolus Morrison (Table 5). A pairwise difference comparison showed a maximum of 0.1% sequence difference in the D2-D3 region of 28S between M. matsumurae. M. resinosae, and M. thunbergianae (Table 6). This is less than the 0.8% recorded within M. acalyptus, 0.7% within M. bisetosus and 0.9% within M. gallicolus (Table 6). Maximum parsimony reconstruction revealed no phylogenetic structure among the individuals of M. matsumurae. M. resinosae, and M. thunbergianae. However, the clade containing M. matsumurae, M. resinosae and M. thunbergianae had 100 percent bootstrap support and Bayesian posterior probabilities value of 100 (Booth, Cook, and Gullan, unpublished data).

Morphology.—Many coccidologists have treated *M. matsumurae* and *M. resinosae* as synonyms based on morphology and life history data (Herbert 1921, Morrison 1928, Ray 1982, McClure 1983b, Kosztarab 1996) but no formal synonymy has been published

Morphological Characters	Character States				
Size De de Showe	(a) under 3 mm; (b) typically larger than 3 mm				
Body Snape	(a) clougate-ovoid; (b) ovoid with two parallel lobes; (c) club shaped				
Dorsum					
Bilocular tubular duct distribution	(a) on apical part of abdomen; (b) in rows on entire body				
Cicatrix bands	(a) absent; (b) 1–4 bands; (c) ≥ 5 bands				
Cicatrix diameter	(a) <9 μ m; (b) 9–20 μ m; (c) ≥25 μ m				
Venter					
Legs	(a) absent; (b) reduced; (c) fully developed				
Antennal segmentation	(a) 2–3; (b) 4–8; (c) 9				
Segment 5 of antennae with 1–2 fleshy setae	(a) absent; (b) present				
Long trochanter setae	(a) 1 long setae; (b) 2 long setae; (c) 0 setae				
Long setae near coxae	(a) absent; (b) present				
Long setae midventrally on abdominal segments V–VII	(a) absent; (b) present				
Abdominal spiracles	(a) 3 pairs; (b) >3 pairs				
Multilocular disk pores	(a) absent; (b) present				
Setae in marginal abdominal bands of bilocular ducts	(a) absent; (b) present				

Table 3. Morphological features of adult females examined for cladistic analysis.

(see Ben-Dov 2005). Below we formally synonymize these three names. No discernible and consistent morphological differences were observed among specimens identified as *M. matsumurae*, *M. resinosae*, and *M. thunbergianae*. A review of the morphology of the adult females for a larger cladistic study (Booth, Cook and Gullan, unpublished) shows the three species to be identical based on 14 characters, including pore types, antennal morphology, and setal characters, typically used to distinguish species of *Matsucoccus* (Table 3). The description of *M. thunbergianae* recognizes this similarity (Miller and Park 1987), but notes that the main differences lie in the morphology of the adult male and several biological characteristics, as we explained in the introduction. The morphological differences among the males of the three species are primarily size differences. However, there is substantial overlap among the three species in the size ranges for all morphological features measured by Miller and Park (1987), including: penial sheath length, aedeagus length, length of antennal

Table 4. Genes and associated primers used for molecular analyses.

Gene	Region	Primer Sequence (5'-3')	Primer Name	Primer Source
18S	24–585	CTGGTTGATCCTGCCAGTAG CCGCGGCTGCTGGCACCAGA	18S–2880 18S–B	Tautz et al. (1988) von Dohlen and Moran (1995)
28S	D2–D3 expansion region	GAGAGTTMAASAGTACGTGAAAC TCGGARGGAACCAGCTACTA	C S3660 A335	Dowton and Austin (1998) Whiting et al. (1997)
	D10 expansion region	GAATGGATTAACGAGATTCTCAA CACAATGATAGGAAGAGCC	None None	Modified from Dietrich et al. (2001) Dietrich et al. (2001)

Species		Number of Polymorphic Sites within Individuals	Number of Polymorphic Sites within Species
M. acalyptus			
	JMB 037	0	5 sites + two indels
	JMB038	1	
	JMB040	0	
M. bisetosus			
	JMB013	0	6 sites: no indels
	JMB026	1	
	JMB029	0	
M. gallicolus			
	JMB023	0	1 site: no indels
	JMB024	1	
	JMB036	0	
M. matsumurae;	M. resinosae; M.	thunbergianae	
(matsumurae)	JMB014	1	4 sites: no indels
	JMB047	1	
(resinosae)	JMB025	1	
	JMB030	3	
(thunbergianae)	JMB021	1	

Table 5. Genetic differences among species for DNA sequences 18S and 28S.

segments II–X, hind femur length, hind tibia length, forewing length, ratio of length of femur/length of tarsus, and length of longest tubular duct on abdominal segment VII.

Bean and Godwin (1955) differentiated adult females of M. matsumurae and M. resinosae based on life history and a subtle morphological disparity concerning the position at which the trachea enters the thoracic spiracles in the intermediate or cyst instar (Bean and Godwin 1955). Herbert (1921) had redescribed M. matsumurae based on both Japanese and American material. However, Herbert based his description partly on American material collected by Mr. J.G. Sanders from the host species P. rigida and P. virginiana. These pines are both known hosts of M. gallicolus, and not hosts of M. resinosae (Ben-Dov 2005). As a consequence of this confusion with M. gallicolus, Morrison (1928) even suggested that M. matsumurae may be indigenous to the Atlantic seaboard of the USA. Later, Morrison (1939) recognized this error and, in his original description of M. gallicolus, noted: "This is the insect which was figured and

described (in part) by Herbert under the name *matsumurae*." Ray (1982) also lists Herbert's *M. matsumurae* as a synonym of *M. gallicolus*. This information was not included in the recent catalogue of the Margarodidae (Ben-Dov 2005).

Tang and Hao (1995) questioned the species concept of M. matsumurae used by American authors, partly because of the confusion created by Herbert's (1921) and Morrison's (1928) mixing up of M. matsumurae and M. gallicolus, and also because they surmised that there may be two species of Matsucoccus in Japan. Tang and Hao (1995) suggested that M. thunbergianae might be synonymous with Kuwana's (1905, 1907) concept of M. matsumurae, and that M. resinosae and M. liaoningensis Tang may be synonyms. They based their argument on purported differences in biology and adult body size of the two species pairs, but they were selective in their use of morphological data and their assertions cannot be supported.

In addition, certain morphological features in *Matsucoccus* can vary in response to environmental conditions. For example, Miller and Park (1987)

	M.	M. acalvatus	M. acalyntus	M.	M. acalyntu	M.	M.	M.
	(JMB002)	(JMB037)	(JMB038)	(JMB039)	(JMB040) (JMB013)	(JMB026)	(JMB029)
M. acalyptus (JMB002)								
M. acalyptus (JMB037)	0.001							
M. acalyptus (JMB038)	0.001	0.000						
M. acalyptus (JMB039)	0.004	0.003	0.003					
M. acalyptus (JMB040)	0.007	0.006	0.006	0.008				
M. bisetosus (JMB013)	0.111	0.109	0.111	0.107	0.112			
M. bisetosus (JMB026)	0.109	0.108	0.109	0.106	0.110	0.000		
M. bisetosus (JMB029)	0.115	0.114	0.116	0.112	0.116	0.007	0.007	
M. gallicolus (JMB023)	0.137	0.137	0.136	0.133	0.136	0.117	0.117	0.118
M. gallicolus (JMB024)	0.129	0.128	0.127	0.124	0.128	0.111	0.111	0.114
M. gallicolus (JMB036)	0.129	0.128	0.127	0.124	0.128	0.111	0.111	0.114
M. matsumurae (JMB047)	0.097	0.095	0.097	0.094	0.098	0.032	0.031	0.037
M. matsumurae (JMB014)	0.098	0.097	0.098	0.095	0.100	0.034	0.032	0.038
M. resinosae (JMB025)	0.099	0.097	0.098	0.095	0.100	0.034	0.033	0.038
M. resinosae (JMB030)	0.097	0.095	0.097	0.094	0.098	0.033	0.031	0.037
M. thunbergianae (JMB021)	0.099	0.098	0.099	0.096	0.100	0.034	0.033	0.039
	M. gallicolus (JMB023)	M. gallicolus (JMB024)	M. gallicoh) (JMB03	A us matsur 6) (JMI	1. murae m B047)	M. atsumurae (JMB014)	M. resinosae (JMB025)	M. resinosae (JMB030)
M. gallicolus (JMB024)	0.007							
M. gallicolus (JMB036)	0.009	0.000						
M. matsumurae (JMB047)	0.115	0.108	0.108					
M. matsumurae (JMB014)	0.117	0.110	0.110	0.0	00			
M. resinosae (JMB025)	0.115	0.108	0.108	0.0	01	0.001		
M. resinosae (JMB030)	0.116	0.108	0.108	0.0	00	0.000	0.000	
M. thunbergianae (JMB021)	0.118	0.111	0.110	0.0	00	0.000	0.001	0.000

Table 6. Pairwise differences table (uncorrected): D2–D3 region of 28S.

examined the overwintering and summer generations of both *M. matsumurae* from China and *M. resinosae* from the U.S.A. and showed that the adult females of the overwintering generation of both species had more multilocular pores and larger cicatrices than the summer populations (Miller and Park 1987). Furthermore, morphological plasticity in body size and additional features has been observed for other species of *Matsucoccus* (Boratynski 1952, Ben-Doy 1981).

A fourth species of *Matsucoccus*, *M. pini* (Green), is found on a member of the *Pinus* subsection, namely *Pinus sylvestris* (Green 1925). This species is distributed throughout Europe and differs only subtly from *M. matsumurae* (Boratynski

1952, Foldi 2004). Boratynski (1952) indicates in his published key to the genus that the main difference between M. matsumurae and M. pini is the width of the dorsal cicatrices, the number of peripheral loculi in the multilocular pores, the host tree, and the country of origin. Foldi (2004) states that M. matsumurae and M. pini differ in the length of the bilocular tubular ducts and the number of multilocular pores at the apex of the abdomen. We examined the paralectotype females of M. pini housed at the BMNH and their morphology falls within the range of variation of M. matsumurae. Foldi (2004) states that the average body size for M. pini is 2.8 mm long, which is less than we recorded for

the specimens of *M. matsumurae* that we measured, however, Foldi also provides a greater body size range for *M. matsumurae* (2.5–4.5 mm long).

No specimens of M. pini were available for molecular analysis, but given the evidence of seasonal plasticity in size of cuticular features in Matsucoccus, the synonymy of M. pini with M. matsumurae seems likely. Other species that should be examined in this context are the Chinese species M. dahuriensis Hu and Hu described from P. sylvestris var. mongolica (Hu and Hu 1981), M. liaoningensis ex P. tubulaeformis (Tang 1978), M. vunnanensis Ferris ex P. yunnanensis (Ferris 1950), and the Russian species M. boratynskii Bodenheimer and Neumark ex P. svlvestris (Bodenheimer and Neumark 1955). These host Pinus species all belong to the same Pinus subsection (Gernandt et al. 2005) as M. matsumurae and appear morphologically similar to it based on available drawings of the adult females.

Matsucoccus matsumurae (Kuwana)

- *Xylococcus matsumurae* Kuwana 1905: 91; Kuwana 1907: 209 (described again as "n. sp.").
- *Matsucoccus matsumurae:* Cockerell 1909: 56 (change of combination).
- *Matsucoccus resinosae* Bean and Godwin 1955: 166. New synonymy.
- Matsucoccus thunbergianae Miller and Park 1987: 50. New synonymy.

Type material.—Syntypes of *Xylococcus matsumurae* Kuwana: JAPAN: Tokyo, at Sugamo, on bark of the trunk of pine-tree; collected May 20, 1903. The type specimens of *X. matsumurae* were destroyed in an earthquake in 1923 (Kuwana 1925, Tang and Hao 1995). Tang and Hao (1995) incorrectly refer to a holotype and paratypes of *X. matsumurae*; there is no evidence that Kuwana ever designated types and the so-called "paratypes" were collected 14 years after Kuwana's first description of the species. The latter specimens were collected by Kuwana outside of Tokyo, Japan, in 1919, whereas Kuwana's original collection was from Sugamo, Tokyo.

Holotype of Matsucoccus resinosae Bean and Godwin, adult female: USA: Connecticut, Easton, on Pinus resinosa, June 2, 1948, collected by George H. Plumb. label also with number "50.2156" (USNM). In their original description, Bean and Godwin (1955) referred to an adult female holotype as well as paratypes of different stages. However, no slides of the type series (all in the USNM) bear any label indicating which adult female is the designated holotype. There are two slides of adult females with collection data matching those given for the holotype in the original description; one slide has four adult females and the other has five, but neither slide has a type label of any kind. In the absence of an identifiable holotype, Ray (1982), in his unpublished dissertation, chose one specimen as the primary type and clearly indicated this information on the slide, but incorrectly labeled it "lectotype" instead of holotype. Here we properly label the previously unlabeled holotype (as recommended by F. Christian Thompson, personal communication to P. J. Gullan): the specimen is on the slide that has four adult females and is the second adult female from the right of the data label (body length: 4.2 mm; width: 2.2 mm). Paratypes of M. resinosae: various life stages including adult females (see Bean and Godwin 1955, page 169 for paratype information).

Holotype of *Matsucoccus thunbergianae* Miller and Park, adult female: SOUTH KOREA: Kohung, Chollanam-do, on *Pinus thunbergiana* (now *P. thunbergii*), collected December 1984, lab reared April 1984, collected by S.C. Park (USNM). Paratypes: 26 adult females, 36 adult males, 5 pupal males, 8 third-instar males, 25 first-instar nymphs: similar data to holotype (see Miller and Park 1987, page 50, for paratype information).

Diagnosis.—The adult female of M. matsumurae can be diagnosed by the following features: body 3.1-4.1 mm long, elongate-ovoid in shape; bilocular tubular ducts distributed in segmental rows on entire dorsum: 5 dorsal cicatrix bands on abdominal segments III to VII. cicatrix diameter 8-14 µm; antennae with 9 segments, segment V of antennae without fleshy setae: legs fully developed. one long (80-100 µm) trochanter seta, long setae (25-34 µm) near coxae on all pairs of legs; 7 pairs of abdominal spiracles; cluster of multilocular disk pores on ventral apex of abdomen; long setae (26-40 µm) midventrally on abdominal segments V-VII, and setae present in marginal abdominal bands of bilocular ducts.

CONCLUSION

Molecular and morphological data as well as host use, sex pheromones, and biogeography support the formal synonymy of *M. matsumurae*, *M. resinosae* and *M. thunbergianae*. The name *Matsucoccus matsumurae* (Kuwana) has nomenclatural priority. Additional species that should be considered for synonymy include *M. pini* and several other Eurasian species.

ACKNOWLEDGMENTS

L. Cook (School of Botany and Zoology, The Australian National University, Canberra) assisted with alignment and interpretation of the nucleotide sequences; D. Miller and D. Creel (Systematic Entomology Laboratory, ARS, USDA, Beltsville, Maryland) arranged the loan of specimens from the Coccoidea collection of the USNM; D. Miller also generously hosted a visit by J. Booth to the USNM Coccoidea collection in March 2005 and provided information about material held there; F. Thompson (Systematic Entomology Laboratory, USDA, Washington D.C.) provided nomenclatural advice. We also are grateful to S.-C. Park (Department of Entomology, Forest Research Institute, Tongdaemun-gu, Seoul) for specimens from South Korea; X. Yingping (The College of Life Science and Technology, Shanxi University, Taiyuan) for specimens from China; and J. Kelley (Mount Pinos Ranger District, California), M. Callan (New York State Department of Environmental Conservation. New Paltz). and C. Maier (Connecticut Agricultural Experiment Station, New Haven), who collected material in the U.S.A. J. Martin (The Natural History Museum, London) arranged the loan of the type specimens of M. pini. S. Takagi (Graduate School of Agriculture, Hokkaido University) provided information on Kuwana's type material. T. Kondo (UC Davis) collected specimens in Japan, translated some Japanese literature, and read a draft of the manuscript; T. K. Oin (Biosecurity Australia) translated some Chinese text: G. Morse (UC Davis) commented on a draft of the molecular results; D. Miller and C. Ray, Jr. also made valuable comments on the manuscript. The Department of Parks and Recreation, California, provided permission to collect in state parks. This research was supported by grant DEB-0118718 from the U.S. National Science Foundation (Partnerships for Enhancing Expertise in Taxonomy program) to P.J. Gullan and by a University of California Davis Center for Biosystematics Grant to J. Booth for molecular work.

LITERATURE CITED

- Bean, J. L. and P. A. Godwin. 1955. Description and bionomics of a new red pine scale, *Matsucoccus resinosae*. Forest Science 1: 164–176.
 - . 1971. Red pine scale. Forest Pest Leaflet 10: 1–16.

Ben-Dov, Y. 1981. Redescription of *Matsucoccus josephi* Bodenheimer and Harpaz (Homoptera: Coccoidea: Margarodidae). Israel Journal of Entomology XV: 35–51.

. 2005. A Systematic Catalogue of the Scale Insect Family Margarodidae (Hemiptera: Coccoidea) of the World. Intercept Ltd., Wimborne, U.K., 400 pp.

, D. R. Miller and G. A. P. Gibson. 2005. ScaleNet. www.sel.barc.usda.gov/scalenet/ scalenet.htm.

- Bodenheimer, F. S. and S. Neumark. 1955. The Israel Pine *Matsucoccus (Matsucoccus josephi* nov. spec.). Keren Kayemeth le Israel Afforestation Dept, Jerusalem, 122 pp.
- Boratynski, K. L. 1952. Matsucoccus pini (Green, 1925) (Homoptera: Coccoidea: Margarodidae): Binomics and external anatomy with reference to the variability of some taxonomic characters. Transactions of the Royal Entomological Society of London 103: 285– 326.
- Cheng, H. Y. and W. J. Ming. 1979. Population dynamics and biological control of *Matsucoccus matsumurae* (Homoptera: Margarodidae). Acta Entomologica Sinica 22: 149–155.
- Chung, Y. J., Y. S. Park, T. S. Chon, S. C. Shin and J. D. Park. 2000. Dispersal pattern of the black pine bast scale, *Matsucoccus thunbergianae* (Homoptera: Margarodidae), in Korea. Journal of Korean Forestry Society 89: 306–309.
- Cockerell, T. D. A. 1909. The Japanese Coccidae. Canadian Entomologist 41: 55–56.
- Cook, L. G., P. J. Gullan and H. E. Trueman. 2002. A preliminary phylogeny of the scale insects (Hemiptera: Sternorrhyncha: Coccoidea) based on nuclear small-subunit ribosomal DNA. Molecular Phylogenetics and Evolution 25: 43–52.
- Dietrich, C. H., R. A. Rakitov, J. L. Holmes, and W. C. Black, IV. 2001. Phylogeny and the major lineages of Membracoidea (Insecta: Hemiptera: Cicadomorpha) based on 28S rDNA sequences. Molecular Phylogenetics and Evolution 18: 293–305.
- Doane, C. C. 1959. Circular 207: The Red Pine Scale. Connecticut Agricultural Experiment Station, New Haven, 7 pp.
- Downie, D. A. and P. J. Gullan. 2004. Phylogenetic analysis of mealybugs (Hemiptera: Coccoidea: Pseudococcidae) based on DNA sequences from three nuclear genes, and a review of the higher classification. Systematic Entomology 29: 238–259.
- Dowton, M. and A. D. Austin. 1998. Relationships among the microgastroid wasps (Hymenoptera: Braconidae): Combined analysis of 16s

and 28s rDNA genes and morphological data. Molecular Phylogenetics and Evolution 10: 354–366.

- Duda, E. J. 1977. Status of the red pine scale Matsucoccus resinosae (Homoptera: Margarodidae). Journal of the New York Entomological Society 85: 171–172.
- Ferris, G. F. 1950. Report upon scale insects collected in China (Homoptera: Coccoidea), Part I. Microentomology 15: 1–34.
- Foldi, I. 2004. The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). Annales de la Société Entomologique de France 40: 145–168.
- Gernandt, D., G. Lopez, S. Garcia and A. Liston. 2005. Phylogeny and classification of *Pinus*. Taxon 54: 29–42.
- Gill, R. J. 1993. The Scale Insects of California, Part 2: The Minor Families (Homoptera: Coccoidea). California Department of Food & Agriculture, Sacramento, 241 pp.
- Green, E. E. 1925. Observations on British Coccidae, IX. Entomologist's Monthly Magazine 61: 34–44.
- Herbert, F. B. 1921. The genus *Matsucoccus* with a new species. Proceedings of the Entomological Society of Washington 23: 15–22.
- Hibbard, B. E., G. N. Lanier, S. C. Park, Y. T. Qi, F. X. Webster and R. M. Silverstein. 1991. Laboratory and field tests with the synthetic sex pheromone of three *Matsucoccus* pine bast scales. Journal of Chemical Ecology 17: 89–102.
- Hu, Y. and J. Hu. 1981. A new species of *Matsucoccus* in Heilongjiang Province (Homoptera: Margarodidae). Journal of Forest Science 2: 178–180.
- Kosztarab, M. 1996. Scale Insects of Northeastern North America: Identification, Biology, and Distribution. Virginia Museum of Natural History, Martinsville, 650 pp.
- Koteja, J. 1984. The Baltic amber Matsucoccidae (Homoptera: Coccinea). Annales Zoologici (Warsaw) 37: 437–496.
- ———. 1986. Matsucoccidae (Homoptera, Coccinea), living fossils. Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri 43: 41–44.
- Kuwana, S. I. 1905. A new *Xylococcus* in Japan. Insect World 9: 91–94.

 . 1907. Coccidae of Japan, II. A new *Xylococcus* in Japan. Bulletin of the Imperial Central Agricultural Experiment Station, Japan 1: 209–212.

. 1925. The Diaspine Coccidae of Japan, II. Bulletin of Agriculture and Commerce, Imperial Plant Quarantine Station 2: 1–42.

Lanier, G. N., Y. T. Qi, J. R. West, S. C. Park, F. X. Webster and R. M. Silverstein. 1989. Identification of the sex pheromone of three *Matsucoccus* pine bast scales. Journal of Chemical Ecology 15: 1645–1659.

- McClure, M. S. 1976. Colonization and establishment of the red pine scale *Matsucoccus resinosae* (Homoptera: Margarodidae) in a Connecticut, USA plantation. Environmental Entomology 5: 943–947.
 - . 1977. Population dynamics of the red pine scale *Matsucoccus resinosae* (Homoptera: Margarodidae): The influence of resinosis. Environmental Entomology 6: 789–795.
 - —. 1983a. Population dynamics of a pernicious parasite: Density-dependent vitality of red pine scale. Ecology 64: 710–718.
 - —. 1983b. Temperature and host availability affect the distribution of *Matsucoccus matsumurae* (Homoptera: Margarodidae) in Asia and North America. Annals of the Entomological Society of America 76: 761–765.
 - —. 1987. Potential of the Asian predator, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), to control *Matsucoccus resinosae* Bean & Godwin (Homoptera: Margardodidae) in the United States. Environmental Entomology 16: 224–230.
- Miller, D. R. and S. Park. 1987. A new species of *Matsucoccus* (Homoptera: Coccoidea: Margarodidae) from Korea. Korean Journal of Plant Protection 26: 49–62.
- Morrison, H. 1928. A classification of the higher groups and genera of the coccid family Margarodidae. United States Department of Agriculture Technical Bulletin 52: 239 pp.
- Park, S. C., J. R. West, L. P. Abrahamson, G. N. Lanier and R. M. Silverstein. 1986. Crossattraction between two species of *Matsucoccus*. Extraction, bioassay, and isolation of the sex pheromone. Journal of Chemical Ecology 12: 609–617.
- Plumb, G. H. 1950. A new and serious insect pest of red pine. Connecticut Agricultural Experiment Station, Special Circular 1950: 1–4.
- Providence Water Supply Board. 2005. www. provwater.com/forestry_mgmt.htm.
- Rambaut, A. 1996. Se-Al: Sequence Alignment Editor. Available at http://evolve.zoo.ox.ac.uk.
- Ray, C. H. J. 1982. Revision of the Genus Matsucoccus (Homoptera: Coccoidea: Margarodidae) in North America. Auburn University, Auburn, 295 pp.

— and M. L. Williams. 1984. Two new species of *Matsucoccus* (Homoptera: Margarodidae) from Arizona, USA and Mexico with a key to species in North America. Annals of the Entomological Society of America 77: 765–769.

- . 1991. Two new species of *Matsucoccus* Cockerell (Homoptera: Margarodidae) similar to *Matsucoccus alabamae* Morrison. Proceedings of the Entomological Society of Washington 93: 186–192.
- Swofford, D. L. 2003. PAUP* Phylogenetic analysis using parsimony (*and other methods), ver. 4. Sinauer Associates, Sunderland, Massachusetts.
- Taketani, A. 1972. Studies on a margarodid scale Matsucoccus matsumurae (Kuwana) (Hemiptera, Coccoidea) Part I. Bionomics. Bulletin of the Government Forest Experiment Station 246: 1–9.
- Tang, F. T. 1978. Discussion on *Matsucoccus* matsumurae with description of a new species. Acta Entomologica Sinica 21: 164–170.
- and J. J. Hao. 1995. The Margarodidae and others of China (Homoptera: Coccinea). Chinese Agricultural Science Technology Press, Beijing, 738 pp.
- Tautz, D., J. M. Hancock, D. A. Webb, C. Tautz and G. A. Dover. 1988. Complete sequences of the ribosomal rRNA genes of *Drosophila melanogaster*. Molecular Biology and Evolution 5: 366–376.
- Von Dohlen, C. D. and N. A. Moran. 1995. Molecular phylogeny of the Homoptera: A paraphyletic taxon. Journal of Molecular Evolution 41: 211–223.
- Whiting, M. F., J. C. Carpenter, Q. D. Wheeler and W. C. Wheeler. 1997. The Strepsistera problem: Phylogeny of the holometabolous insect orders inferred from 18s and 28s ribosomal DNA sequences and morphology. Systematic Biology 46: 1–68.
- Young, B., D. R. Miller and M. S. McClure. 1984. Attractivity of the female sex pheromone of Chinese *Matsucoccus matsumurae* (Kuwana) to males of *M. matsumurae* in Japan and to males of *M. resinosae* Bean and Godwin in the United States (Margarodidae, Coccoidae, Homoptera). Contributions of the Shanghai Institute of Entomology 4: 1–20.